8. Contributions to Morphology. Ichthyopsida.—No. 1. On *Ceratodus forsteri,* with Observations on the Classification of Fishes. By Prof. T. H. Huxley, Sec. R.S.

[Received January 4, 1876.]

Two specimens of *Ceratodus forsteri* have come into my possession within the last two years. The first was kindly placed at my disposal by the Secretary of this Society some time ago; but I was unwilling to dissect it until I had a second. This desideratum was supplied by my friend Sir George MacLeay, who, on a recent visit to Australia, was kind enough to undertake to obtain a *Ceratodus* for me, and fulfilled his promise by sending me a very fine and well-preserved fish, rather larger than the first. The first was 32 inches long, the second only 30 inches, though a considerably stouter fish.

I need hardly say that I have little to add or qualify in the general description of the exterior structure given by so accomplished and experienced an ichthyologist as Dr. Günther*. Only in one point do I find my interpretation of the facts widely discrepant from his; and that is in regard to the position of the external nostrils.

Dr. Günther says, "As in *Lepidosiren,* there are two nasal apertures on each side, both being situated within the cavity of the mouth."

That anterior nasal apertures should be situated, in any sense, "within the cavity of the mouth" would be so singular a deviation from the otherwise universal rule, that the anterior nares of vertebrated animals are situated outside the mouth, on the surface of the head, that conclusive evidence must be producible before the anomaly can be admitted to exist; and, so far as my observations go, that conclusive evidence is not only wanting, but the contrary is demonstrable.

In *Ceratodus,* it is easily seen that the anterior nares are not occluded when the mouth is shut by the apposition of the edges of the mandible to the palate. The anterior nares, in fact, lie altogether outside and in front of the contour of the mandibles, on the under concave surface of the anterior part of the head. The median portion of the margin of this region of the head must not be confounded with the upper lip, with which it has nothing to do. The maxillary portion of the upper lip is, in fact, represented only by a fold of the integument, which begins on the outer side of the anterior nostril, and extends back to the angle of the gape, where it passes into the lower lip. The præmaxillary, or internasal, portion of the upper lip is represented by a delicate fold of the integument, disposed in a transverse arch in front of the vomerine teeth, which it separates from the inner boundary of the anterior nares. The outer and posterior portion of the lower lip is produced into a free process, which is folded back against the jaw, and extends for about two thirds of the distance from the angle of the mouth to the symphysis, ending by a rounded free edge.

* "Description of *Ceratodus,*" Phil. Trans. pt. ii. 1871.

Thus the anterior nares can in no sense be said to open into the cavity of the mouth, inasmuch as they lie outside the præmaxillary portion of the upper lip, and are not enclosed by the maxillary portion of that lip. They are not even placed between the upper and the lower lips, inasmuch as the vaulted flap, on the underside of which they lie, is not the upper lip, but the anterior part of the head.

In *Lepidosiren*, the anterior nares are closer to the anterior margin of the head than in *Ceratodus*, and the præmaxillary lip is represented only by a papillose ridge, in which the integument of the underside of the head, between the anterior nares, terminates posteriorly. Otherwise the disposition of the nostrils is quite as in *Ceratodus*; and when the mouth is shut, the nostrils open on the underside of the head, in front of it and of the rudimentary præmaxillary portion of the upper lip.

The disposition of the nasal apertures in the Dipnoi is essentially Selachian *. In the common Dogfish (*Scyllium*), for example, the anterior contour of the head answers to the anterior contour of the head of *Ceratodus*. The mandibular and maxillary lips are similarly disposed; and the external nares are placed on the sides of the head in a similar position. But the præmaxillary part of the upper lip is much larger and more prominent; and its outer edges (septal alæ), instead of being continued into the maxillary lip, to form the floor of the nasal passage, are separated from it by a fissure, which communicates with the nasal cavity. This fissure is overlapped by the septal alæ; and thus an incomplete nasal passage, which opens posteriorly into the cavity of the mouth, is constituted.

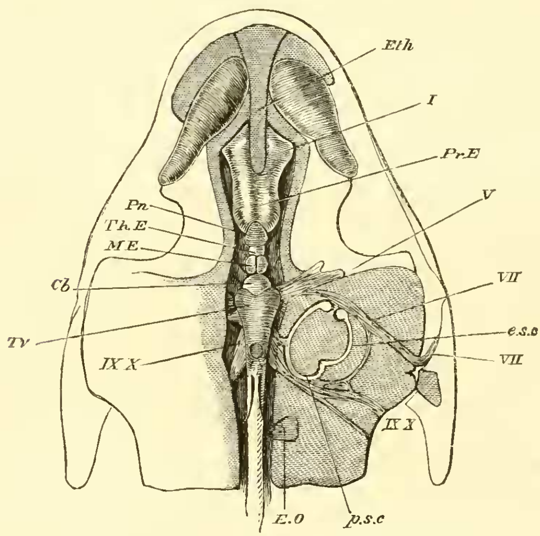
Still more instructive is the comparison of the nasal passages of *Ceratodus* with those of *Cestracion* and *Chimæra*. In *Cestracion*, the external nostrils lie just outside the mouth, the lower lip coming into contact with the maxillary and præmaxillary portions of the upper when the mouth is shut. The anterior end of the maxillary lip is folded in, and passes into the external part of the *ala nasi*, which has a thickened edge, and ends in a continuation of the free fold of the lip. The inner *ala nasi* is the outer part of the internasal or præmaxillary part of the upper lip. It also ends in a free edge, which is rolled inwards. The septal ala and the maxillary ala do not unite; but a groove is left between their convex edges, which answers to part of the groove which leads from the nose into the mouth in Dogfish and other Plagiostomes. But the greater part of this groove is represented by a canal formed by the convoluted septal ala, which is open on its dorsal aspect, and communicates, in front, with the cavity of the olfactory sac. Behind, the free edge of the septal ala has a curious fringe; and when the mouth is shut, this fringe overlaps the edge of the mandible. The free edge of the septal ala bounds a large opening, the posterior nostril, which is situated, as in *Ceratodus*, at the point of junction between the vomerine and the palatine teeth. Consequently, when the mouth is shut, there is a free passage for water through this incompletely closed nasal canal.

* See the excellent observations of Gegenbaur, 'Kopfskelet der Selachier,' p. 224 *et seq.*

An arrangement of a very similar character exists in *Chimæra*. Here the nasal septum is very narrow, but widens out below, where, as the præmaxillary lip, it overlaps the vomerine teeth. The free edge of the septal ala is curved in, as in *Cestracion*. Meeting it is an inward process of the maxillary lip, which abuts against the septal ala in the same way as the maxillary ala does in *Cestracion*. Outside this, again, is another flap-like process of the maxillary lip, which overhangs the foregoing when the maxillary lip is in place. Between the præmaxillary lip and the maxillary lip is the nasal passage, open ventrally as in *Cestracion*; and an interval between the vomerine and palatine teeth above and the mandibular tooth below (the posterior nostril) places this passage in free communication with the oral cavity.

It is obvious that if the septal and the maxillary alæ in *Scyllium*,

Fig. 1.



Ceratodus forsteri. Dorsal view of the brain *in situ*.

Pr E, *lobus communis* of the prosencephalon; *Th.E*, Thalamencephalon; *Pn*, pineal gland; *ME*, mesencephalon (the median groove is somewhat too strongly marked); *Cb*, cerebellum; *Tv*, tela vasculosa over the fourth ventricle; *e.s.c*, *p.s.c*, external and posterior semicircular canals; I, V, VII, IX, X, cerebral nerves; *E.O*, exoccipital ossification. The general contour of the chondrocranium is given; on the right side the cartilage has been sufficiently removed to show the anastomosis of the seventh and ninth nerves, the auditory organ, and other deep-seated parts. With respect to this and the other figures, I may remark that my object has been to make accurate diagrams drawn to scale, and not pictures.

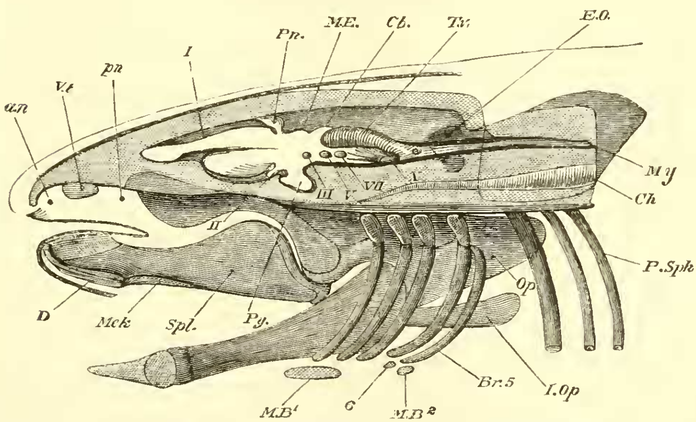
Cestracion, and *Chimæra* united along the middle line, such a nasal passage as exists in *Ceratodus* would be the result. Compared with

Ceratodus, the Elasmobranchs mentioned are hare-lipped; and as regards the position of the external nostrils, *Cestracion* and *Scyllium* are intermediate between *Chimæra* and *Ceratodus.*

It may be asked, what is the use of a nasal passage and of internal nares in a purely branchiate animal? Without actual experiment it is hard to give a definite answer to this question; but I will venture upon two suggestions. In the first place, these communications between the cavity of the mouth and the exterior must permit slow respiration to take place when the jaws are shut; and it is easy to imagine that this, under many circumstances, may be an advantage.

In the second place, the large olfactory sacs of these animals suggest that the sense of smell is of value to them; and the communication of the nasal passages with the mouth must enable them to do what they could not do otherwise—namely, accelerate the rapidity of the contact of odoriferous particles with the Schneiderian membrane at will. The fish with posterior nasal apertures, in fact, can "sniff" effectually, while that operation could only be very imperfectly performed by compression and dilatation of the walls of the olfactory

Fig. 2.



Ceratodus forsteri. Left lateral view of the brain *in situ.*

The details of the structure of the dorsal region of the spinal column are omitted. *Ch,* notochord; *E.O,* exoccipital ossification; *P.Sph,* parasphenoid; *V.t,* vomerine teeth; *an, pn,* positions of the anterior and posterior nares; *Op,* operculum; *I.Op,* interoperculum; *Spl,* splenial, and *D,* dentary bones of the mandible; *Mck,* Meckel's cartilage; *M.B*¹, *M.B*², anterior and posterior mesobranchials; *Br.* 5, fifth branchial arch; 6, nodule of cartilage, which possibly represents a rudimentary sixth arch; *Py,* pituitary body. The other letters have the same signification as in the preceding figure. The suprascapular bone is shown in place; and its contour is given as if the anterior part of the vertebral column were transparent.

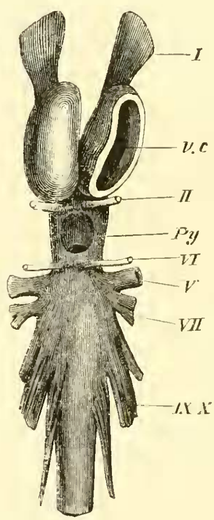
sacs in the absence of any second opening. Probably the second opening so generally present in the olfactory sacs of the Teleostei, and the naso-palatine canal of the Marsipobranchs, have a similar physiological significance. In *Ceratodus* there is the further physiological relation to aerial respiration ; and in all the higher Vertebrata the nasal passages are concerned in sniffing and breathing.

With respect to the internal structure of *Ceratodus,* I shall confine my remarks, in the present communication, to the brain, the skull, and the pectoral limbs. *Ceratodus* is, in fact, the most surprisingly suggestive animal I have ever had occasion to study ; and the attempt to comprehend the morphological significance of the organs I have mentioned has led me so far, that I must defer the consideration of other parts of its organization to another occasion.

I. *The Brain.*

I had no great hope of finding the brain in a state fit for examination in my specimen of *Ceratodus* ; and in fact the cerebral substance and that of the nerves are in a very friable condition. But, by great good fortune, the *pia mater* is so very dense and tough, that it has held the cerebral substance in place ; and thus not only the external form, but somewhat of the internal structure of the brain could be satisfactorily determined.

Fig. 3.



Ceratodus forsteri. Underview of the brain (nat. size).

I, olfactory, II, optic, VI, third nerve (?) ; V, VII, IX, X, roots of the trigeminal, portio dura, auditory, glossopharyngeal, and pneumogastric nerves ; *v.c*, one of the lateral ventricles of the *lobus communis,* laid open from below.

The brain is represented from above in fig. 1, from the left side in fig. 2, and from below in fig. 3.

The brain of *Ceratodus* nearly fills the cranial cavity, the interspace left between it and the walls of the latter being, to a great extent, occupied by a peculiar reticulated tissue. The *medulla oblongata* is long and slender, but widens, anteriorly, in the region of the fourth ventricle. This cavity is arched over by a *tela vasculosa* (*Tv*, figs. 1 and 2), separated into two lateral convexities by a slight median depression. In front, each convexity is continued into a blind rounded cornu, which lies over the origin of the fifth and seventh auditory nerves. The two cornua diverge, and the cerebellum is continued backwards as a triangular lamella between them. The cerebellum is relatively very small, being represented merely by the thin arched roof of the anterior part of the fourth ventricle. In front of it is a rounded elevation, obscurely divided by a longitudinal depression into two. These are the only indications of the optic lobes of the mid brain, or mesencephalon. In front of this is the fore brain. The hinder division (or thalamencephalon) is narrower than the mesencephalon, and passes below into the infundibulum, which terminates in the large, oval, flattened, pituitary body (*hypophysis*). This is lodged in an excavation of the cartilaginous floor of the skull representing the *sella turcica*.

Dorsally, the thalamencephalon is continued upwards and forwards into the subcylindrical peduncle of the pineal gland (*epiphysis* or *conarium*). This is a large heart-shaped body, the base of which is turned downwards and backwards. The apex is connected by fibrous and vascular tissue with a depression in the cartilaginous roof of the skull.

Next follows the largest division of the brain, answering to the cerebral hemispheres and the olfactory lobes. The former are represented by a single oval *lobus communis*, the middle area of the roof of which is occupied by a broad thick *tela vasculosa*. From the anterior dorsal aspect of the prosencephalon proceeds, on each side, the large olfactory lobe, which, flattening in front, and becoming obliquely truncated, terminates against the posterior walls of the olfactory sacs. A backward prolongation of the mesethmoid cartilage separates the two lobes. In the lateral view of the brain (fig. 2) the manner in which the olfactory lobes take their origin from the dorsal aspect of the prosencephalon is well seen. The short and thick infundibulum, terminating in the flattened oval pituitary body, and the origins of the second, third, fifth, eighth, ninth, and tenth nerves are shown.

The ventral view (fig. 3) displays the origins of the small optic nerves (II) which arise close together from the floor of the thalamencephalon. Whether any *chiasma* exists could not be ascertained.

In the middle line of its ventral aspect the prosencephalon presents a deep longitudinal fissure, lodging anterior cerebral arteries. The walls of the fissure have been separated by turning the left division of the prosencephalon to one side; and the floor of the ventricle (*v.c*), which is contained in the prosencephalon, has been removed.

When the dorsal wall of the brain was cautiously laid open by a median section, it was found to contain one large ventricular cavity the separation of which into fourth and third ventricles was indicated only by slight constrictions of the roof and side walls. The large ventricle of the prosencephalon is partially separated into two chambers by a median septum, formed by the infolding of its ventral wall; and the spacious ventricle of each olfactory lobe opens into the dorso-lateral part of each of these chambers.

The place and mode of origin of the olfactory and of the optic nerves have already been mentioned.

The third nerve is indicated in the figure; but I am somewhat doubtful as to the nature of the cord thus marked.

No fourth or sixth nerve was observed.

The fifth arises by a single large cylindrical root just below the anterior end of the cornu of the tela vasculosa of the fourth ventricle. The seventh and eighth leave the medulla by a common root just behind this; and the roots of the ninth and tenth nerves, divided into three bundles, arise from a tract at the sides of the medulla which extends from the last to the hinder limit of the *tela vasculosa*, and incline obliquely backwards to their exit.

The brain of *Ceratodus* is very singular and interesting, inasmuch as it presents resemblances to that of the Marsipobranchii on one side, to that of the Ganoids and Amphibia on another, and to that of the Chimæroids and Plagiostomi on a third.

As in the brain of the Marsipobranchii, the pineal gland is relatively very large, with its pointed dorsal end inclined upwards and forwards, and the roof of the fourth ventricle is almost entirely formed by the *tela vasculosa*; but, as in the Ganoidei and Amphibia, the cerebellum is larger than in the Lampreys. In *Ceratodus* it is similar to, though proportionally less than, that of *Lepidosteus*, and still more like that of *Polypterus*. In the proportions of the thalamencephalon the brain of *Ceratodus* resembles that of the Sturgeon and that of the Ray; while in the representation of the cerebral hemispheres, or prosencephalon, by a large imperfectly divided *lobus communis*, from the dorso-lateral regions of which the olfactory lobes take their rise, the brain of *Ceratodus* presents a feature hitherto known, so far as I am aware, only in the Plagiostomi*. Thus, in its cerebral characters, *Ceratodus* occupies a central place in the class Pisces.

The development of the cerebral hemispheres in Plagiostome fishes differs from the process by which they arise in the higher Vertebrata. In a very early stage, when the first and second visceral clefts of the embryo of *Scyllium* are provided with only a few short branchial

* So far as I can judge from the examination of a small but well-preserved specimen of *Lepidosiren annectens*, for which I am indebted to Mr. Sclater, the brain of this fish is similar, in all essential respects, to that of *Ceratodus*. The figure of the brain of *Lepidosiren* given by Prof. Owen in his 'Anatomy of Vertebrates' is susceptible of interpretation in this sense. Hyrtl's description and figure of the brain of *Lepidosiren paradoxa* (Abhandlungen der königlichen böhmischen Gesellschaft, Bd. iii. 1845), on the other hand, leave me in doubt whether, apart from its curious asymmetry, the brain of this fish does or does not present important differences from that of *Ceratodus* and that of *Lepidosiren annectens*.

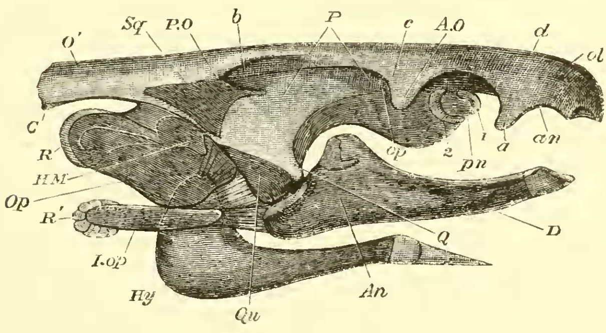
filaments, the anterior cerebral vesicle is already distinctly divided into the thalamencephalon (from which the large infundibulum proceeds below, and the small tubular peduncle of the pineal gland above, while the optic nerves leave its sides) and a large single oval "vesicle of the hemispheres." On the ventral face of the integument covering these are two oval depressions, the rudimentary olfactory sacs.

As development proceeds, the vesicle of the hemispheres becomes divided by the ingrowth of a median longitudinal septum, and the olfactory lobes grow out from the posterior lateral regions of each "ventricle" thus formed, and eventually rise onto the dorsal faces of the hemispheres, instead of, as in most Vertebrata, remaining on their ventral sides. I may remark that I cannot accept the views of Miklucho-Maclay, whose proposal to alter the nomenclature of the parts of the Elasmobranch's brain appears to me to be based upon a misinterpretation of the facts of development.

II. *The Skull.*

Dr. Günther * distinguishes in the skull an "inner cartilaginous capsule and an outer incomplete osseous case, to which again some outer cartilaginous elements are appended. In the former the con-

Fig. 4.



Ceratodus forsteri. Lateral view of the chondrocranium, with most of the bones and fibrous tissues removed.

ol, position of the olfactory sac; *an*, *pn*, position of the anterior and posterior nares; *a*, process of the cranial cartilage, *d*, between the two; 1, 2, upper labial cartilages; *op*, optic foramen; *A.O*, antorbital process; *P.O*, postorbital process; *P.Q*, palato-quadrate process; *Sq*, *Qu*, remains of the bony plate which lies on the outer side of this process; *O.C*, occipital prolongation of the chondrocranium roofing over the branchial cavity; *D*, dentary; *An*, angular; *Hy*, hyoid; *I.op*, interoperculum; *Op*, operculum; *R*, *R'*, cartilages representing hyoidean rays; *HM*, hyo-mandibular.

fluence of cartilage is so complete, that no distinct divisions are traceable by sutures; its parts can be designated only by reference to the locally corresponding bones of the teleosteous skull."

* *L. c.* p. 521.

This would seem to imply that the chondrocranium of vertebrated animals is formed by the coalescence of parts analogous to those which compose the bony skull of osseous fishes. As a matter of fact, however, the chondrocranium is never formed of such elements, but is built up, at a very early stage of embryonic development, by the union of primitively distinct parachordal, otic, and pleural elements*, which in no way correspond with the bones of the teleostean skull. And when Dr. Günther subsequently (*l. c.* p. 522) speaks of "three groups of superficial labial cartilages," "the upper labial," the "supraorbital," and the "lower labial," the discrimination of such cartilages must, I think, be regarded merely as regional anatomy; and it must not be supposed that they have any thing to do with the cartilages to which the same names are applied in other fishes, several of which exist in *Ceratodus*, and will presently be described.

When the osseous and merely fibrous structures are carefully removed, I find that the chondrocranium (figs. 4, 2, and 7) consists of a continuous cartilaginous mass, the interorbital region of which is much narrower than any other part, produced inferiorly and laterally into two stout suspensorial or palato-quadrate processes, with the pulley-shaped ventral ends of which the strong Meckelian cartilages are articulated. Anteriorly the orbits are bounded by the *antorbital processes* (*A.O*), which curve downwards in front of the eye. From these autorbital processes the cartilage is continued forwards to form the evenly curved roof of the ethmoidal region and its contained nasal chambers, and, bending down on all sides, ends in a free edge, which is slightly concave opposite each anterior nasal opening (*an*, fig. 4), and much more deeply excavated opposite the posterior nares (*pn*, fig. 4). The small process (*a*) which lies between the two excavations in question is connected by a strong fibrous band with the antorbital process (*A.O*), and this, by the ossified bar described by Dr. Günther, with the *postorbital process* (*P.O*); but these structures have nothing to do with the chondrocranium. Behind the orbits, the skull suddenly widens out into two broad periotic masses, which lodge the auditory labyrinth. Anteriorly and ventrally these processes are continued into the suspensorial pillars (*Qu*); while behind they pass into thin but wide cartilaginous plates (*O, C*, fig. 4), which roof over the chambers in which the branchiæ are lodged.

I thought at first that *Ceratodus* had no labial cartilages; but at length I discovered two small upper labial cartilages in their right places, namely in the region of the nostrils.

One of them (1, figs. 4 and 5) lies in the roof of the mouth, just in front, and on the inner side of, the posterior nasal aperture. It is fixed to the mesethmoidal cartilage (*M.E*) by fibrous bands, and is broader behind than in front. The inner edge of this cartilage is concave, the outer convex, and it has a nearly horizontal direction.

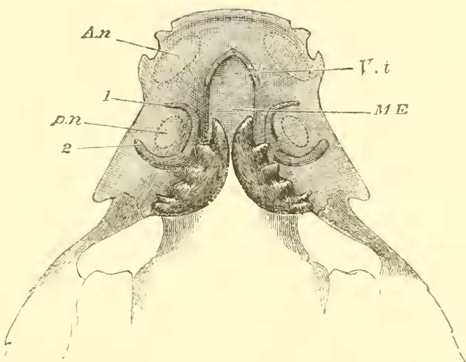
The second cartilage (2, figs. 4, 5, 7) is stouter, and lies behind, and on the outer side of, the posterior nasal aperture. Its dorsal end is attached to the base of the skull and anterior part of the

* "On the Structure of the Skull &c. of *Menobranchus lateralis*," P. Z. S. 1874.

palato-quadrate cartilage just above the middle of the palatine tooth. It thence descends with an outward convexity and inward concavity, and terminates in the upper lip near the angle of the mouth.

Dr. Günther states (*l. c.* p. 524) that "the body of the mandible is persistent cartilage; but its entire outer and inner surfaces are covered by bone, forming an articular and a dentary piece. . . . . . The articular and dentary bones meet near the top of a low but strong coronoid process, and again at the symphysis, which is formed by fibrous tissue, and may easily be separated by the knife . . . . In front of the jaw the cartilage is expanded into a slightly concave lamella (lower labial cartilage)."

Fig. 5.



Ceratodus forsteri. Underview of the skull, showing the vomerine teeth (*V.t*), the palatine teeth, the mesethmoid cartilage (*M.E*), and the upper labial cartilages (1, 2) in place. The dotted lines *An*, *p.n* indicate the form and position of the anterior and the posterior nares.

I find a persistent Meckelian cartilage, such as that here described; but as, after careful removal of the ensheathing bones, I have been unable to discover any separation between this lamellar expansion and the rest of the cartilage, I am in doubt whether the lamella represents the lower labial cartilage or not. The analogy of the Frog, however, leads one to suspect that distinct lower labial cartilages may exist in the young *Ceratodus*.

Dr. Günther does not mention a third ensheathing bone (figs. 2 and 4, *D*) which is united by suture with the other two, and lies on each side of the symphysis on the ventral face of the mandible. It is a flat plate, of a triangular form, with a thick rugose inner edge for the attachment of the symphysial ligament. Its posterior edge is thin and concave; its external edge is also thin and overlaps the bone termed "articular" by Dr. Günther, uniting with it by a squamous suture. The outer half of its dorsal aspect is smooth, and helps to support the ventral face of Meckel's cartilage; the inner or symphysial half presents a broad rough triangular surface, which extends on the inner side of the symphysial end of Meckel's cartilage, and unites with a corresponding surface furnished by the expanded symphysial end of the bone, termed "dentary" by Dr. Günther. I cannot doubt that this bone is the representative of the true "dentary" element; nor is there any question in my mind that Dr. Günther's "dentary" is the true "splenial" element, while his articular answers to the "angular" piece of the vertebrate mandible. In the attachment of the tooth to the splenial, and not to the dentary, element, *Ceratodus* presents an interesting and important feature of resemblance to *Siren* and to larval Salamanders on the one hand, and, on the other, to *Polypterus*.

The splenial element in this Ganoid resembles that of *Ceratodus*, not only in bearing teeth, but in form, position, and relative size. In a young specimen of *Polypterus* I find that the splenial does not extend continuously to the symphysis, but that, between its anterior termination and the latter, there are two short and broad bony plates developed in the fibrous tissue which overlies Meckel's cartilage; these bear teeth, and correspond with the expanded symphysial end of the splenial in *Ceratodus*. *Polypterus* has a true *articulare*, from which Meckel's cartilage is continued. The *angulare* is much shorter, and the *dentale* much longer than in *Ceratodus*.

The hyoidean and opercular apparatus present characters of singular interest. Dr. Günther says that "on the hinder side of the tympanic pedicle*, near its base, there is a small round tubercle, for the suspension and articulation of the hyoid arch (pl. xxxiv. fig. 3, *v*)."

I presume that this "small round tubercle" of the suspensorial expansion of the cranium is the small cartilage marked *H.M* in figs. 4 and 6. But this is neither a process of the suspensorium, nor does it articulate with, nor take the principal share in, suspending *Hy*, which is Dr. Günther's "hyoid arch."

In fact it is, as fig. 6 shows, a distinct, though small, four-sided, flattened cartilage, the anterior and ventral angle of which is produced into a short conical process (*Sy*). Its anterior edge is firmly united with the skull, just where the cranium proper passes into the suspensorium. At this point there is a triangular vacuity filled with fibrous tissue, through which the posterior division of the seventh nerve passes (figs. 1 and 6, VII). The outer face of the cartilage is loosely connected with the operculum (*Op*); and the conical process (*Sy*) is imbedded in the dorsal and posterior part of the powerful ligament (*h.s*) (corresponding with the hyosuspensorial ligament in *Menobranchus*†) by which *Hy* is mainly kept in place.

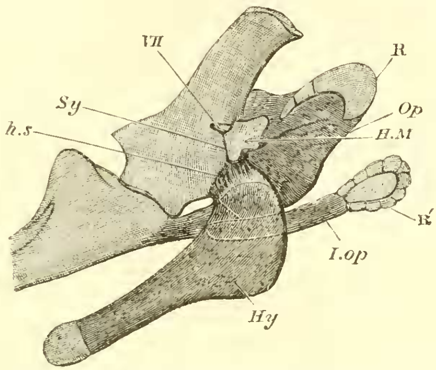
It is obvious that this little cartilage is the homologue of the hyomandibular element of the hyoidean arch of other fishes, the small conical process being the rudimentary *symplectic*, and, therefore, that

* It is surely to be regretted that any writer of authority should retain the misleading name of "tympanic pedicle" for a part the total distinctness of which from the "tympanic bone" of the higher Vertebrata has now been so copiously demonstrated.

† P. Z. S. 1874, pl. xxix. figs. 1 and 2.

it is itself the dorsal element of the hyoidean arch, attached in its normal position, as its relations to the seventh nerve show. The hyoidean cornua are very strong, and consist of a cartilaginous axis almost completely ensheathed by bone. The dorsal end of each is

Fig. 6.



Ceratodus forsteri. Inner view of the right hyoidean arch (*Hy*), with the opercular apparatus and part of the suspensorium and of the mandible.

H.M. hyomandibular cartilage; *Sy*, its symplectic process; *Op*, operculum; *I.op*, interoperculum; *R*, *R'*, cartilaginous rays attached to the inner face of the operculum and interoperculum; VII, exit of the posterior division of the seventh nerve; *h.s*, hyosuspensorial ligament (immediately beneath it is the mandibulo-hyoid ligament).

attached by the strong hyo-suspensorial ligament aforesaid to the suspensorium; but another very strong round ligament (answering to the *mandibulo-hyoid ligament* of *Menobranchus**) connects the dorsal end of the hyoidean cornu with the angle of the mandible (figs. 4 and 6).

Thus the hyoidean arch of *Ceratodus* strikingly resembles that of a Plagiostome on the one hand, and that of an Amphibian on the other. And the small hyomandibular presents a form and connexions which are strikingly similar to those of the *suprastapedial* cartilage in the Sauropsida†, which, on a former occasion, I showed to be the summit of the hyoidean arch and the homologue of the mammalian incus.

In describing the operculum Dr. Günther says (*l. c.* p. 525), "A small movable piece of cartilage is found inside of the articulary groove of the opercle (pl. xxxiv. figs. 2 and 3, *k*): it is a rudiment of the præoperculum."

Neither the figures referred to nor the account given enable me to be certain that they apply to the cartilaginous structures I am about

* P. Z. S. 1874, *ibid.*

† "On the representatives of the Malleus and Incus of the Mammalia in other Vertebrata," P. Z. S. 1869.

to describe, and which are to be found not only on the inner face of the operculum, but on that of the interoperculum*.

On the inner side of the former and projecting beyond its free edge is a curved band of cartilage divided into several portions†. One of these, that nearest the hyomandibular, is conical and bent at an angle to that which follows it. The terminal plate is broad and crescentic, and, on one side, was subdivided towards its free edge. On the inner face of the posterior end of the interoperculum (*I.op.*) there is an oval cartilage surrounded by eight or nine smaller nodules.

These cartilages represent the cartilaginous branchiostegal rays of Plagiostomes, which are often subdivided into two groups—a dorsal group attached to the hyomandibular, and a ventral group to the cornual division of the hyoid arch.

The *præoperculum* of Fishes and the *squamosal* of the higher Vertebrata are represented by the bone *Sq*, termed "tympanic lamina" by Dr. Günther. I have marked the lower piece, which was distinct on the specimen represented in fig. 4, *Qu*; but in another specimen I can find no subdivision, and I am disposed to think that the division arose from an accidental dismemberment of a squamosal (or præoperculum) corresponding with that of *Menobranchus* (P. Z. S. 1874, pl. xxix. fig. 1, *Sq*), and that there is no true quadrate in *Ceratodus*. I can discover no ossification of the substance of the articular extremity of the suspensorium, such as occurs in the Amphibia. The pterygopalatines and the vomers, which last are represented only by the bases of the two vomerine teeth, are similar in their form and relations to the corresponding bones of Urodele Amphibia.

With respect to the branchial apparatus, Dr. Günther (*l. c.* p. 526) says that it "does not differ from that of Teleostean fish, but is entirely cartilaginous. There are five branchial arches, the last rudimentary and attached to the base of the fourth. There is no peculiar modification of any part of this apparatus; and the middle pieces have the usual groove for the reception of the vessels and nerves."

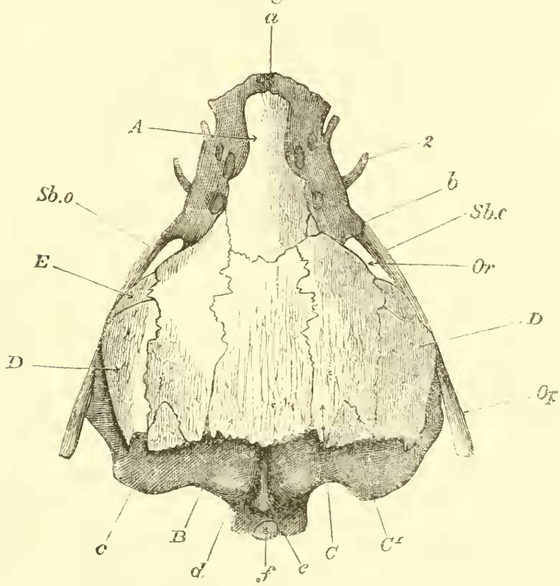
I find that each of the anterior four branchial arches consists of a long ventral and a short dorsal piece of cartilage: the former pieces are united by ligament at their ventral ends, the third and fourth curving forwards in this part; they are connected by joints surrounded by ligaments with the dorsal pieces (fig. 2). In the median

* Dr. Günther terms the bone here named interoperculum, "suboperculum." He says (*l. c.* p. 525) that to the lower edge of the operculum "is attached by fibrous tissue the long styliform *suboperculum*, terminating at a considerable distance from the mandibulary joint." It is quite true that the bone in question is thus attached to the operculum; but a much more important connexion takes place between its ventral end and the angle of the jaw, by means of strong ligamentous fibres which run into the hyomandibular ligament. It thus more closely resembles the interoperculum of Teleosteans than it does the suboperculum.

† In a specimen of the skull of *Ceratodus*, for which I am indebted to my friend Mr. F. M. Balfour, the curved band of cartilage of the operculum is not subdivided, and the interopercular cartilages are divided less regularly and differently on the two sides.

ventral line, between the ends of the ventral pieces, lie two cartilages—an anterior elongated and spindle-shaped (*M.B*[1]), which is connected by a strong ligament with the median piece of the hyoid arch, and a posterior rounded nodule (*M.B*[2]) at some distance from the foregoing. The fifth arch consists of a single piece of cartilage curved forwards and united with the principal branchial of the fourth arch, both above and below; in front of it, close to the ventral end of the fifth arch, was a small nodule of cartilage, which is probably a rudimentary sixth arch (6).

Fig. 7.



Ceratodus forsteri. Dorsal aspect of the skull.

a, the anterior end of the chondrocranium; *b*, the antorbital process of the chondrocranium; *c*, its suprabranchial expansion; *d*, lateral elevations of the occiput; and *e*, median ridge, with the surface for the attachment of the anterior fin-ray; *f*, articular surface for the second fin-ray; *A*, anterior median bone; *B*, posterior median bone; *C*, inner lateral bone; *C″*, distinct ossification on the posterior extremity of this bone; *D*, outer lateral bone (squamosal); *E*, a separate ossification on the left side; *Op*, operculum; *Or*, orbit; *Sb.o*, suborbital bones; 2, the posterior upper labial cartilage.

As Dr. Günther has pointed out, the osseous shield which covers the dorsal aspect of the skull consists of two median bones (fig. 7, *A*, *B*), one anterior and one posterior, which he terms "ethmoid" and "scleroparietal," and of two pairs of lateral bones, the "frontals" internally (fig. 7, *C*) and the "tympanic laminæ" externally (fig. 7, *D*). In my specimens the anterior half of the anterior median bone (*A*) has a different shape from that given in Dr. Günther's plate xxxiv. fig. 1, and its margins are very well defined. Moreover, in one specimen, the hinder end of each inner lateral bone is completed by a distinct ossification (C'). There is also a separate ossification (E) on the left side, on what corresponds with the front part of the outer lateral bone on the right side. Doubtless these bones are subject to much individual variation.

The fibrous band which extends, below the eye, between the antorbital process and the ventral end of the suspensorium contains three suborbital bones. The anterior of these, trihedral, is connected by its broad base with the antorbital process; the middle bone is slender and elongated; the posterior is broad, flattened from side to side, and its hinder edge is fixed by ligamentous fibres to the outer face of the suspensorium and of the squamosal.

The *basal bone* of Dr. Günther is the parasphenoid. It extends backwards, beyond the limits of the proper cranium, into the region of the vertebral column, to a point just beyond the attachment of the third pair of ribs. But there is at least one vertebra in front of that which bears the first pair of ribs. In *Ceratodus*, as in the Sturgeon and other Ganoids, several anterior vertebræ have coalesced with one another and with the skull; or, probably, it would be more accurate to say that the investing mass of the notochord has not become differentiated into vertebræ for this extent. Nevertheless the posterior boundary of the skull can be strictly defined by the interspace between the exit of the pneumogastric and that of the next following, or first spinal, nerve.

It is to the outer surface of this interspace that the anterior edge of the "suprascapular" element of the pectoral arch is fixed by strong ligamentous fibres (fig. 2). Just in front of the boundary between the skull and the vertebral column, and therefore in the side walls of the former, there lies, deep in the substance of the cartilage, a hollow cone of bone ($E.O$) It is wider above and externally than below and internally, where its end lies above the notochord. This appears to be an exoccipital ossification, such as is to be found in greater state of development in *Lepidosiren, Polypterus*, and *Menobranchus*.

The skull of *Ceratodus* is, as might be expected (and as Dr. Günther has pointed out), extremely similar to that of *Lepidosiren*. In fact, beyond differences in the proportions of its various parts, the more extensive fenestration of the roof of the olfactory capsules in *Lepidosiren*, and the absence, so far as my investigations have yet gone, of the hyomandibular cartilage in the latter genus, the cartilaginous elements of the skull are the same in the two cases.

As to the superadded bones, the parasphenoid, the rudimentary vomers, and the pterygopalatine plates correspond in the two genera. The exoccipitals are much larger in *Lepidosiren*. The descending process or præopercular part of the squamosal is best developed in *Lepidosiren*, whilst its dorsal part (proper squamosal) is larger in *Ceratodus*.

In both, there are two opercular bones, an operculum and an interoperculum; and in *Lepidosiren*, as in *Ceratodus*, there are cartilaginous plates attached to the inner faces of these bones.

The branchial apparatus of *Lepidosiren* differs from that of *Ceratodus* mainly in the greater number of complete branchial arches.

It can hardly be doubted that the bone *D* of *Ceratodus* is represented, though incompletely, by the supraorbital of *Lepidosiren*, while the bony nasal shield of the latter corresponds very closely with the anterior median bone (*A*) of *Ceratodus*. The posterior boundary of the bone, however, lies further back in *Ceratodus* than it does in *Lepidosiren*. The argument of Dr. Günther that the posterior median bone (*B*) in *Ceratodus* is not the homologue of the parieto-frontal of *Lepidosiren*, because it lies above the muscles, while the latter is situated beneath them, is weighty against the identification of the bones in question; and, in other respects, the parieto-frontal of *Lepidosiren* is very unlike the "scleroparietal" of *Ceratodus*.

When the comparison of the cranial and facial bones of *Ceratodus* with those of the Vertebrata is extended beyond the limits of the Dipnoi, the determination of their homologues is beset with many difficulties. *Polypterus* has an anterior and a posterior median shield in the roof of the skull, which at first seem to correspond with those of *Ceratodus*; these shields are each formed by the union of two bones, which are evidently comparable to the frontals and parietals of the higher Vertebrata, while the frontals unite with a pair of broad nasals which cover the olfactory sacs. The apices of the posterior triangular edges of these bones reach back to near the level of the middle of the orbits; and the frontal bones are continued forwards on each side of them. Between the two nasal bones there is a median ossification which lies upon the mesethmoidal cartilage and spreads out in front, ending by a broad edge which articulates with the præmaxillæ.

The median bone, the piscine "ethmoid," occupies the same position as the anterior median bone of *Ceratodus* would do if the ethmoidal region were reduced to the proportions it has in *Polypterus*. Therefore, from this point of view, the determination of the bone as "ethmoid" by Dr. Günther seems fully justifiable; and the inner lateral and the median posterior bones would seem to represent the frontal and parietal bones of *Polypterus*.

On the other hand, the many points of resemblance between *Ceratodus* and the Amphibia suggest the comparison of the anterior and posterior median bone to the frontals of *Menobranchus*, and of the inner lateral bones to the parietals of this Amphibian. The forward extensions of the latter, at the sides of the frontals, are especially noticeable in comparison with the anterior extremities of the inner lateral bones of *Ceratodus*. On the whole, I am inclined to think that *Polypterus* is the better guide in the interpretation of the cranial bones of *Ceratodus*, though the difference between the bones of *Ceratodus* and those of the Crossopterygian ganoids, all of which are readily reducible to the Polypterine type, is very considerable.

In other respects the skull of *Cerotodus* finds its closest parallel among the Amphibia, especially such Urodela as *Menobranchus**, and the Anura in their tadpole state.

* See P. Z. S. March 17, 1874.

I have already indicated the chief points of resemblance to the amphibian skull, and need not recapitulate them here. The most important feature is the manner in which the mandibular arch is connected with the skull.

The part of the palato-quadrate cartilage which is united with the skull, between the exits of the fifth and second nerves, answers to the "pedicle of the suspensorium" of the amphibian, while its backward and upward continuation onto the periotic cartilage corresponds with the otic process. As in the Amphibia and in the higher Vertebrata, the mandibular arch is thus attached directly to the skull by that part of its own substance which constitutes the suspensorium. It may thus be said to be *autostylic*.

Among fishes, the only groups which possess an autostylic skull, or in which the dorsal end of the mandibular arch is continuous with the cartilage of the brain-case, are the Chimæroids and the Marsipobranchii.

In *Chimæra*, the general form and connexions of the palato-quadrate cartilage are the same as in *Ceratodus*; but it differs from that of *Ceratodus* as that of the tadpole differs from that of a young Frog, or as that of *Menobranchus* differs from that of *Menopoma*; that is to say, the articular condyle is situated far more forward, and the gape is, in consequence, relatively shorter in the former than in the latter. There are the same large olfactory capsules in both cases. In *Chimæra*, however, these project beyond the termination of the ethmoidal cartilage, while in *Ceratodus* the latter projects beyond the olfactory capsules, which are more lateral in position, more elongated, and, in accordance with the general form of the head, much more depressed.

Just as in *Ceratodus*, the palato-quadrate cartilage of *Chimæra* bears two teeth marked with radiating ridges, while two others, the vomerine teeth, are supported by the ethmoidal cartilage in front of these; and in both cases there is a tooth with radiating ridges on its surface in each ramus of the mandible.

In the disappearance of the notochord and the articulation of the skull with the anterior coalesced vertebræ, the skull of *Chimæra* presents a higher degree of differentiation than that of *Ceratodus*; while it is needless to speak of such aberrant peculiarities as its supracerebral interorbital septum, or the vast crest into which the skull is raised above the anterior part of the brain-cavity. In other respects, however, as in the inclination of the axis of the suspensorium already noted, the skull of *Chimæra* presents lower characters than that of *Ceratodus*. Among these may be reckoned the great size of the upper and lower labial cartilages and the condition of the hyoidean arch, which, except in size and some peculiarities of form, is altogether similar to the four branchial arches which follow it. Like them, it terminates, dorsally, in a flat, expanded, triangular piece, which is connected with the superjacent floor of the skull by muscles and ligaments, but by no direct articulation. The dorsal pieces of the succeeding branchial arches have the same form and attachments, and unite with the ventral segments at a sharp angle. These angles are all connected together by a strong ligament, which is continued to the pectoral arch. Moreover a small styliform cartilage passes from the last angle to the pectoral arch, and is connected with the dorsal end of the fifth branchial arch. It appears to represent the dorsal element of that arch.

Johannes Müller, fully appreciating the importance of the differences between the skull of the Chimæroids and those of other "Elasmobranchii," and sagaciously remarking that "the skull of *Chimæra* is most like that of a tadpole"*, was thereby led to separate the Chimæroids as a suborder of the Elasmobranchii under the name of *Holocephali*. It appears to me that he might have been justified in going still further; for, considering, in addition to the cranial characters, the structure of the vertebral column and of the branchiæ, the presence of an opercular covering to the gills, the peculiar dentition, the almost undeveloped gastric division of the alimentary canal, the opening of the rectum quite separately from and in front of the urinogenital apertures, the relatively small and simple heart, the Chimæroids are far more definitely marked off from the Plagiostomes than the Teleostei are from the Ganoidei.

In all other Fishes, except the Marsipobranchii, the mode of connexion of the mandibular arch with the skull is different from that which obtains in the Chimæroids and the Dipnoi. The palato-quadrate cartilage is no longer continuous with the chondrocranium (though the bony elements of that arch may unite suturally with those of the skull, as in the Plectognathi), but is, at most, united with it by ligament. Moreover the dorsal element of the hyoidean arch, or the hyomandibular, usually attains a large size and becomes the chief apparatus of suspension of the hinder end of the palato-quadrate cartilage with the skull. Skulls formed upon this type, which is exemplified in perfection in Ganoidei, Teleostei, and ordinary Plagiostomes, may therefore be termed *hyostylic*.

But though the typical forms of autostylic and hyostylic skulls, as exemplified, *e.g.*, by a Sturgeon, a Pike, and a Dogfish or Ray, on the one hand, and *Chimæra*, *Ceratodus*, and *Menobranchus* on the other, are thus widely different, certain Plagiostomes present a condition of the cranium which tends to connect the two by a middle form, which may be termed *amphistylic*.

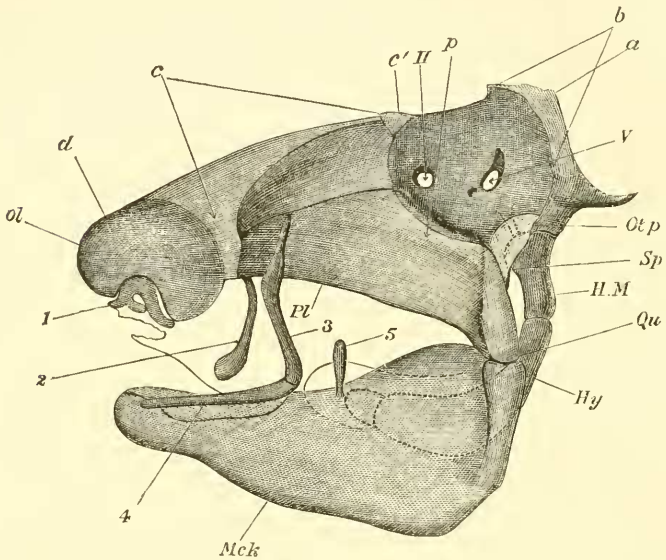
In the amphistylic skull the palato-quadrate cartilage is quite distinct from the rest of the skull; but it is wholly, or almost wholly, suspended by its own ligaments, the hyomandibular being small and contributing little to its support. The embryo amphibian is amphistylic before it becomes autostylic; and, in view of certain palæontological facts, it is very interesting that the link which connects the amphistylic with the ordinary Selachian skull is that of *Cestracion* (fig. 8).

If the palato-quadrate cartilage of *Chimæra* were membranous in the centre, as it is in the tadpole, and if along three lines radiating from this centre the cartilage were converted partly into fibrous tissue and partly into a true joint, the result would be to produce a palato-

* 'Vergleichende Anatomie der Myxinoiden,' erster Theil, p. 150.

quadrate apparatus such as that exhibited by *Cestracion*. The huge palato-quadrate cartilage (*Pl, Qu*) of *Cestracion* is united with the skull in the præorbital region by a joint, and in the orbital region by fibrous tissue, and answers to that part of the palato-quadrate cartilage of *Chimæra* which lies between the nasal capsule and the mandible.

Fig. 8.



Cestracion philippi. Left lateral view of the skull.

a, occiput; *b*, postorbital process; *c*, *c′*, antorbital process; *d*, anterior end of the chondrocranium; *ol*, olfactory capsule; *Ot.p*, otic process, or spiracular cartilage; *Sp*, place of the spiracle; *H.M*, hyomandibular cartilage; *Qu*, articulation of the palato-quadrate cartilage (*Pl, Qu*) with the lower jaw (*Mck*); *p*, part of the palato-quadrate arch which answers to the pedicle of the suspensorium in Amphibia; *Hy*, hyoid; II, foramen for the optic, and V, for the trigeminal nerves; 1, 2, 3, 4, the upper and lower labial cartilages; 5, a small cartilaginous style attached by ligament to the mandibular cartilage.

The small cartilaginous plate (*Ot.p*), which is connected only by ligament with the periotic cartilage above and with the quadrate below, answers to the *otic process* of the Frog's suspensorium. This cartilage lies in the front wall of the spiracle, which in *Cestracion* is situated low at the sides of the head, nearly in a line with the branchial clefts, or in the position which it occupies in fœtal Selachians. Moreover this so-called *spiracular cartilage* bears a rudimentary gill and is so far comparable to any of the branchial arches*.

In possessing this permanent mandibulo-hyoid cleft, or spiracle, which is the homologue of the tympanic cavity and Eustachian tube of the higher Vertebrata, and in the permanence of its rudimentary

* Gegenbaur considers the spiracular cartilage to be a ray of the mandibular arch.

branchia, *Cestracion* exhibits a lower stage of organization than *Chimæra*, in which, as in *Ceratodus*, the mandibulo-hyoid cleft has disappeared. On the other hand, the hyoidean arch presents a form intermediate between that of the ordinary Selachians and that of *Ceratodus* and *Chimæra*. It is stout; and its dorsal element, still retaining a little of its original form, but much thicker and more cylindrical, is no longer united with the skull by ligament and muscle merely, but articulates with a process of the underside of the periotic capsule. Moreover its distal end is connected by strong ligamentous fibres with the posterior end of the palato-quadrate cartilage and with an inward process of the articular end of the mandible (the *sustentaculum* of Gegenbaur).

In fact, the "epibranchial" of the hyoidean arch of *Cestracion* is just beginning to take on a new function, that of suspending the palato-quadrate cartilage and mandible to the skull. It is a true hyomandibular, though small and insignificant relatively to what it becomes in other Plagiostomes, in Ganoids, and in Teleostei.

Had I been acquainted with the skull of *Cestracion* in 1858, I should have been spared the hesitation which I then felt* as to identifying the hyomandibular of Fishes with the summit of the hyoidean arch, and which has subsequently been removed by abundant evidence published by Mr. Parker and myself.

In the general form of the skull, the position and proportions of the olfactory capsules, and the characters of the principal labial and alinasal cartilages, *Cestracion* has a stronger resemblance to *Chimæra* than is exhibited by any other Plagiostomes; and I take it to be one of the lowest of Selachian skulls.

I am aware that in expressing this opinion I am diametrically opposed to Gegenbaur†, whose elaborate study of the Plagiostome skull entitles his opinion to the greatest weight, and who regards *Cestracion* as possessed of one of the highest of skulls in its group, while *Heptanchus* and *Hexanchus* have the lowest.

There is a certain ambiguity about the terms "highest" and "lowest;" but if by the former we understand the most extreme modification of the hyostylic type of skull characteristic of the group, then I should have no hesitation in regarding the skulls of the Rays as the highest of Plagiostome skulls, while *Cestracion* represents a low form of the autostylic type.

Notidanus, on the other hand, appears to me to have an essentially low form of skull, so far as it is more completely amphistylic than any ordinary Plagiostome; but on this low form is superinduced a modification by which it approaches the higher autostylic skull. This is the union of the palato-quadrate arch with the postorbital

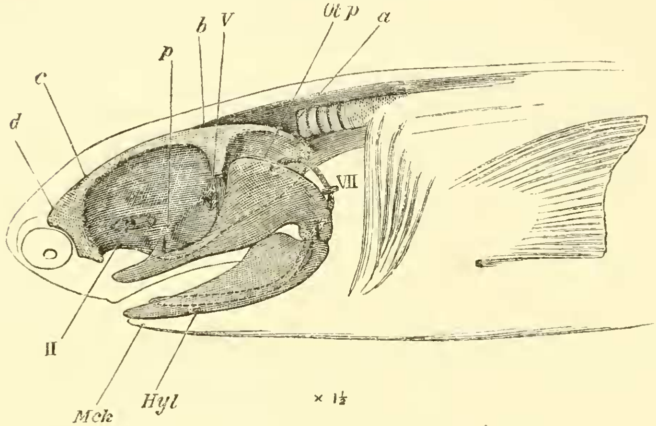
* Croonian Lecture, 1858, and Lectures on the Theory of the Skull, 1864. See also "On the Malleus and Incus," P. Z. S. 1869; 'Manual of Vertebrate Anatomy,' 1871, p. 85; and Mr. Parker's "Memoir on the Development of the Salmon," Phil. Trans. 1872.

† 'Das Kopfskelet der Selachier,' p. 60. In controverting the opinion of Professor Owen that the *Cestracion* is less advanced in cranial development than *Squatina*, Gegenbaur observes, "So möchte ich gerade das Gegentheil behaupten, und nicht etwan bloss bezüglich der Basalverhältnisse des Craniums."

process of the skull—an articulation which, in Prof. Gegenbaur's view, represents the primitive attachment of the mandibular arch, but, in my apprehension, is an altogether secondary connexion.

I am indebted to Dr. Günther for a fœtus of *Notidanus* (*Heptanchus*) *cinereus* in excellent condition; and the examination of the skull (fig. 9), which presents all the characteristic features of the adult*, has confirmed the suspicion which I previously entertained, that the

Fig. 9.



Notidanus cinereus. Left lateral view of the skull. Letters as in the preceding figures. VII, the posterior division of the portio dura.

skull of *Notidanus*, though fundamentally of a low type, is greatly modified so far as the jaws are concerned. What first led me to suspect that this might be the case was the backward position of the articular end of the suspensorium and the relative length of the gape—features in which the skull of *Notidanus* differs from that of ordinary Selachians as an old frog differs from a young one.

The palato-quadrate cartilage of *Notidanus* has an inward process (*p*), which lies in a strong ligamentous band, by which it is attached to the skull between the optic and trigeminal foramina. This answers to the pedicle of the suspensorium in the Amphibia. From this point the palato-quadrate cartilage extends backwards, as a laterally compressed deep plate, the posterior and inferior extremity of which gives attachment to the mandible. The dorsal and anterior angle of this plate is attached only by ligament to the postorbital process, in the fœtus, but appears to articulate therewith in the adult. I think that there can be no doubt that this upward and backward extension of the palato-quadrate cartilage answers to the *otic process* in the amphibian. It has similar relations to the posterior division of the seventh nerve; and between it and the hyoidean arch lies the

* See Gegenbaur, *op. cit.*

spiracle, in correspondence with its homologue the tympano-eustachian passage. The dorsal and posterior edge of this process no less clearly corresponds with the spiracular cartilage in *Cestracion*, otherwise absent in *Notidanus*. The hyoidean arch is attached to the periotic region of the skull. It is very slender; and though closely bound by ligament to the mandibular arch, close to the articulation of the mandible, it can contribute little or nothing to the support of the latter. Remove the great otic process of the palato-quadrate arch of *Notidanus*, and bring its quadrate end further forward, and the result would be a typically amphistylic skull, such as exists in the larval *Siredon* and *Triton**.

The relations of the skulls of *Notidanus*, *Cestracion*, and *Ceratodus* may be thus expressed:—

Notidanus most nearly approaches the amphistylic skull, such as exists in all the autostylic Vertebrata in the embryonic state; but it is considerably altered by the development of a great otic process from the mandibular arch.

In *Cestracion* the palato-quadrate has become massive, and, in the region of the pedicle, is firmly united with the skull, while the otic process is a separate cartilage, connected only by ligament with the postorbital process above and with the palato-quadrate below.

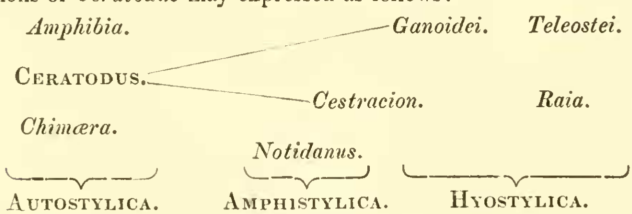
In *Ceratodus* the palato-quadrate has coalesced with the skull both by its pedicle and by its otic process; and the same change occurs in the autostylic skulls of the Amphibia.

In the ordinary Plagiostomes, on the other hand, the palato-quadrate becomes smaller and more freely united with the skull. The otic process (=spiracular cartilage) is smaller, and the hyomandibular takes a larger and larger share in suspending the mandibular arch to the skull, which is therefore eminently hyostylic.

Turning now to osseous fishes, the skull which presents the nearest resemblance to *Ceratodus* is that of *Polypterus*. This will be obvious to any one who studies the excellent description of the chondrocranium of this fish given by Dr. Traquair†.

But in the character of the palato-quadrate arch and the great relative size of the hyomandibular, the skull is as thoroughly and completely hyostylic as is that of any other existing Ganoid or Teleostean.

Thus, having regard only to the structure of the cranium, the relations of *Ceratodus* may expressed as follows:—



* P. Z. S. 1874. pl. xxxi. figs. 1 & 2.

† "The Cranial Osteology of *Polypterus*," Journal of Anatomy and Physiology, 1870.

III. *The Pectoral Limb.*

In the memoir cited, Dr. Günther describes the limbs of *Ceratodus* and their skeleton as follows:—

"The limbs consist of two pairs of paddles, similar in appearance to the termination of the tail; viz. a longitudinal axis, formed by the endoskeleton and muscles and covered with scales, is surrounded by a broad rayed fringe. These paddles are structurally identical with the fins of *Lepidosiren*; only the axis and also the fringe are much dilated. The pectoral and ventral paddles taper to a fine point, the former being longer than the head, the latter rather shorter. The ventral paddles are inserted at a short distance in front of the vent" (p. 515).

"The paddle is joined to the scapular arch by an elongate, flattish, slightly curved cartilage; its proximal end has a glenoid cavity, fitting into the humeral condyle; the joint is simple, free, allowing of a considerable amount of motion, its parts being held together by a ligament fastened round its circumference. This is the only true joint in the limb, all the other parts being fixed to one another by connective tissue. I consider this cartilage to be the forearm; a horizontal section along its longitudinal axis does not show any primary division. The next following cartilage forms the base of the paddle; although externally it appears as a single flat, broad, short piece, unevennesses of its surface indicate that several primary pieces are coalesced in it.

"I am confirmed in this view by a horizontal section, in which the lines of the former divisions are preserved in the shape of tracts of a white connective tissue. Three such divisions may be distinguished, corresponding to the three carpals of most Plagiostomes *. If this determination is correct, then the antibrachial cartilage just described is not represented in that order.

"The remaining framework of the paddle shows an arrangement unique among the Vertebrata. From the middle of the basal cartilage a series of about twenty-six subquadrangular pieces takes its origin, forming a longitudinal axis along the middle of the paddle to its extremity. The pieces become gradually smaller, and are scarcely distinguishable towards the end of the paddle. On the two posterior corners of each piece a branch is inserted, running obliquely backwards towards the margin of the fin; the branches of the first eight or twelve pieces are three-jointed, the remainder two-jointed, the last having no branch at all. Slight irregularities, such as the origin of two branches from one side of a central piece, occur, as also several four-jointed branches being inserted immediately on the basal cartilage" (pp. 532–3).

In general, this description suits the pectoral fins of the specimen I have described very well. Mine, however, has only twenty median cartilages. All but the very last bear lateral rays; but towards the distal end of the fin these become minute, and consist of a single piece. Moreover the distal joints are much more slender, especially

* Pro-, meso-, and metapterygium of Gegenbaur.

the last. A more important point is that the second shows no trace of such divisions as those described by Dr. Günther. To make sure of this I made a thin microscopic section of this cartilage on the right side, and thereby satisfied myself of the homogeneity of the cartilage of which it is composed.

I find no true joint between the proximal median piece and the scapular arch, the connexion between the two being effected by a solid fibrous mass.

Again, the "slight irregularities" in the distribution of the rays, in respect of the median pieces, of which Dr. Günther speaks, are constant peculiarities of no small importance. This becomes obvious when the fin of *Ceratodus* is compared with that of other fishes. But before proceeding to this point I must make a few remarks on the normal and primitive position of the vertebrate limb, and on the changes from that normal position which take place in fishes on the one hand, and the higher Vertebrata on the other, as, for want of attending to this fundamental matter, grave errors have crept into the interpretation of the parts of the limbs of different vertebrates.

The fins occupy the normal position in such a fish as *Scyllium*. When the axis of the body is horizontal the plane of the fin is also horizontal. Its upper surface is covered by a continuation of the dorsal integument, and its lower surface by that of the ventral side of the body. The distinctive spotting of the dorsal aspect in the Dogfish makes this very plain; therefore, to adopt the nomenclature which I some time ago proposed, the convex thick edge of the fin is præaxial, while its concavo-convex thin edge is postaxial, and its two aspects look respectively upwards and downwards.

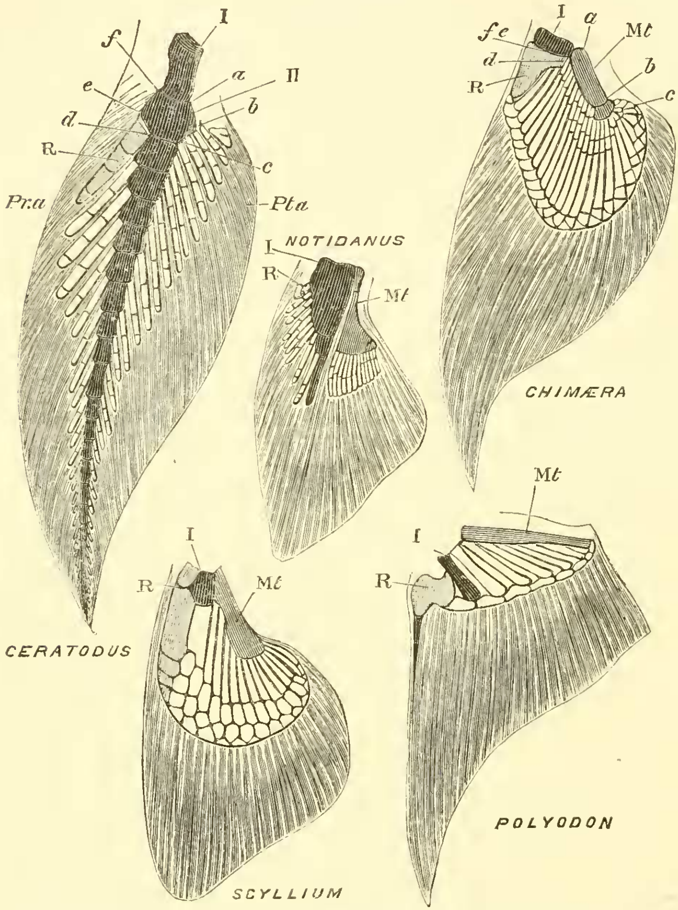
In *Ceratodus*, however, the fin has undergone a rotation upon its axis, in virtue of which its proper ventral surface looks more or less outwards, and its proper dorsal surface more or less inwards; and at the same time the præaxial edge is turned upwards, while the postaxial edge is turned downwards. This is very marked when the fin is applied to the trunk; but the primitive disposition of the surfaces and edges of the limb becomes obvious when the fin is made to stand out at right angles to the axis of the body.

In *Acipenser*, as in any Teleostean fish, the rotation becomes still more marked; and divarication of the fin does not greatly diminish it, by reason of the articulation of the præaxial fin-ray with the pectoral arch at a point higher than the proper glenoid cavity.

When *Ceratodus*, or a Teleostean fish, is placed side by side with a Urodele Amphibian, such as *Menobranchus*, in which the fore limb naturally takes a position nearly parallel with the axis of the trunk, the manus being directed backwards, nothing is more natural than to imagine that the outer and inner aspects and the dorsal and ventral edges of the two correspond.

But a very little consideration will show that nothing can be more erroneous; for the outer surface of the *Menobranchus* limb is its proper dorsal aspect, and the inner surface is its ventral aspect, as will be seen the moment the limb is placed at right angles with the trunk. In fact, though in the amphibian, as in the fish, the limb has undergone a twist, the direction of its rotation is exactly contrary to that which has occurred in the fish. Taking the left limb in each case, the normal fin would have to be turned in the direction of movement of the hands of a watch to bring it to the teleostean position,

Fig. 10.



The left pectoral fins of *Ceratodus forsteri*, *Notidanus cinereus* (fœtal), *Scyllium canicula*, *Chimæra monstrosa*, and *Polyodon folium*.

The præaxial (*Pr.a*) and postaxial (*Pt.a*) margins of all are turned in the same direction; *R*, the præaxial ray (propterygium of Gegenbaur); *Mt*, the metapterygium; I, the basal or proximal joint of the axial skeleton.

while it would have to be turned in the contrary way to bring it into the amphibian position. Hence the præaxial edge in the teleostean fin is dorsal, while in the amphibian limb it is more or less ventral;

and the skeletal elements on the dorsal side of the axis of the fish-fin answer to those on the ventral side of the axis in the amphibian limb.

As Dr. Günther has observed, the contour of the fin in *Ceratodus* is somewhat like that of a sickle. The præaxial edge is convex forwards and rather thicker, especially at its proximal end, than the posterior edge, which is concave backwards in its distal and convex in its proximal half. The apex of the fin is slender and recurved. A rounded and narrowed neck unites the limb with the trunk.

Thus the limb, as a whole, is essentially unsymmetrical when its postaxial and præaxial halves are compared. A corresponding asymmetry is strikingly obvious in the skeleton when it is prepared by removing the integument and muscles of the dorsal face, while the undisturbed condition of the parts is preserved by leaving the ventral integument and muscles untouched (fig. 10).

It will be seen that, on the præaxial side (*Pr.a*), each of the subquadrate segments of the median part of the skeleton, except the first and the terminal segments, gives attachment by its distal angle to a single jointed ray. The proximal or first ray (*R*) is much stouter than any of those which succeed it; and all take a direction approximately parallel to one another, their long axes forming an acute angle with that of the series of median segments. In the distal portion of the fin, the postaxial rays have a similar arrangement, and are only more slender than the præaxial rays. But the second segment bears no fewer than five rays. Of these, the proximal, which is shortest and slenderest, stands out at right angles to the axis of the series of median segments; while the others are gradually inclined at a less and less angle to it. The third segment and the fourth each carry two postaxial rays; the rest have but one.

Dr. Günther's figures show that, in his specimen also, the fourth and the third segments each bore two postaxial rays; but there are only four attached to the second segment, and all these are represented as if they had nearly the same inclination to the axis of the fin as the præaxial rays.

To dwell so strongly upon these minutiæ may seem to be making a great deal of a very small matter; but its importance becomes manifest when the fin of *Ceratodus* is compared with that of other fishes.

In my "Preliminary Essay on the systematic arrangement of the Fishes of the Devonian epoch" *, I made use of the term "Crossopterygian" to express a peculiarity which is very strikingly manifest in the fishes to which I applied it, the fin-rays of the paired fins being disposed, like a fringe, round an oval, or elongated, central space covered with scales. The Crossopterygii, however, were not defined by this character alone; and hence the fact that truly fringed fins are found beyond the limits of that group does not interfere with its perfectly natural character. In strictness, all fishes which possess paired fins are Crossopterygian in so far as the fin-rays always fringe the

* Memoirs of the Geological Survey of the United Kingdom, decade x. 1861.

edges of the fin; and they differ only in the relative extent of the central area, on which the fin-rays do not encroach.

All the Chimæroids and Plagiostomes are eminently crossopterygian so far as their fins are concerned; and therefore we might expect to find in the skeleton of the pectoral fins of these fishes a modification of the skeleton of that of *Ceratodus*. But in most of these fishes the skeleton of the fins has undergone such an amount of metamorphosis that it is difficult to reduce it to the type of *Ceratodus*. In *Notidanus**, however, the skeleton of the pectoral fin affords the key to the nature of this metamorphosis. Here (fig. 10) there is an axial cartilage, the broad proximal end of which articulates with the pectoral arch. Distally it diminishes in diameter, and ends by a truncated face, with which another slender cylindrical cartilage, also axial in position, is articulated.

I take these two cartilages to represent the shrunken axis of the fin of *Ceratodus*. The præaxial basal angle of this axial mass is occupied by a distinct cartilage. Whether this represents the proximal axial cartilage of *Ceratodus*, or whether it is the proximal præaxial ray, is not clear.

The præaxial edge of the principal axial cartilage, at some little distance from this piece, presents a series of notches, with which are articulated a corresponding number of præaxial rays, while, as has been already stated, a single ray is articulated to the base of the terminal axial cartilage. The uppermost or proximal præaxial ray is two-jointed and broader than the others. On the postaxial side there is a triangular cartilage (*Mt*), wide distally, very narrow proximally, where it is connected with the proximal end of the axial cartilages. Twelve postaxial rays are articulated with the wide distal edge of this cartilage. I conceive that this triangular postaxial cartilage is formed by the coalescence of the axial ends of the postaxial rays.

The fin-skeleton of *Notidanus* thus results, in the simplest possible manner, from the shortening of the axis of such a fin-skeleton as that of *Ceratodus* and the coalescence of some of its elements.

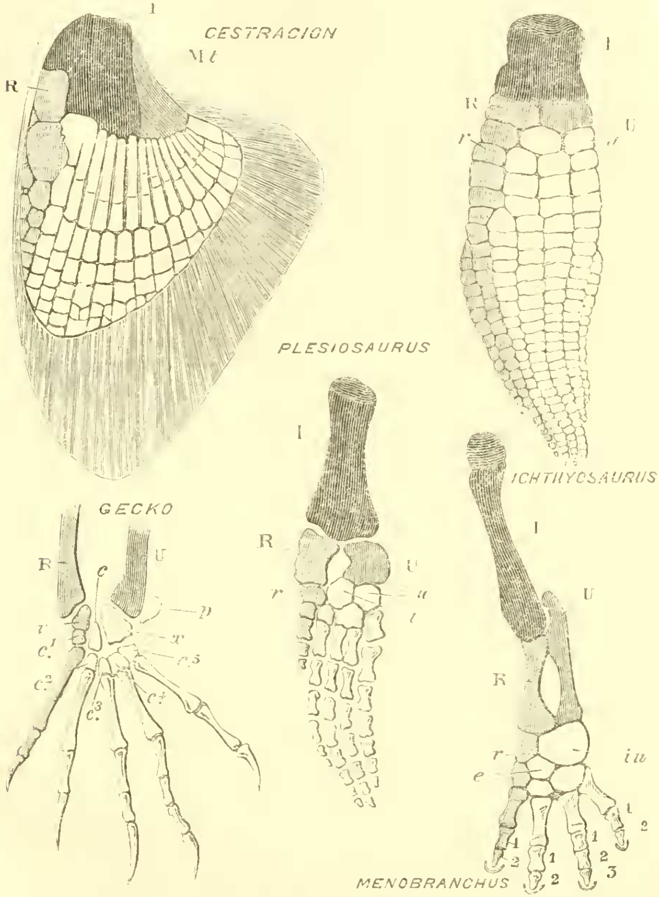
In *Cestracion* (fig. 11) the same process is carried a step further. Here there is a large cartilage (I) which articulates with the pectoral arch by a concave facet, and corresponds with the proximal axial cartilage of *Ceratodus* and *Notidanus*. United by ligament with its hinder concave margin is the triangular postaxial cartilage (*Mt*), which obviously answers to the similarly shaped postaxial cartilage of *Notidanus*, and which bears a series of postaxial rays, of which the first is directed almost at right angles to the axis of the fin, as in *Ceratodus*. The first præaxial ray (*R*) is very large and bifurcates distally. The ray which is attached to the distal angle of the axial cartilage probably answers to the ray-like termination of the axial skeleton in *Notidanus*; but it is not distinguishable from the rest.

In the Dogfish (*Scyllium*) (fig. 10) the further shortening of the axis gives rise to still greater changes. The axial cartilage (*meso-*

* The figure represents the fin of the fœtal *Notidanus* to which I have already referred. The figure of the fin of an adult of the same species given by Gegenbaur (Untersuchungen, Heft ii. Taf. ix. fig. 2) shows essentially the same structure.

pterygium of Gegenbaur, I) is relatively small; but the enlarged postaxial cartilage (*metapterygium, Mt*) has extended upwards along the

Fig. 11.



The left pectoral fin of *Cestracion philippi* (letters as before), the left fore limbs of *Ichthyosaurus, Plesiosaurus, Menobranchus*, and the left manus of *Gecko verus*.

I, humerus; *R*, radius; *U*, ulna; *r*, radiale; *i*, intermedium; *u*, ulnare; *c*, centrale; c^1, c^2, c^3, c^4, c^5, distal carpals; 1, 2, 3, phalanges of *Menobranchus*. In *Gecko* it is uncertain whether *x* represents the intermedium and the ulnare coalesced as in *Menobranchus* (*i u*), or whether *x* is the intermedium and *p* is the ulnare, occupying the place of a pisiform bone.

postaxial face of the first, until it has not only reached the articular surface of the pectoral arch, but furnishes a large part of the articular cavity. In like manner the proximal præaxial ray (*propterygium*, *R*) has ascended along the præaxial face of the axial cartilage, until it also is able to furnish a facet which completes the anterior part of the cup for the condyle of the pectoral arch.

In *Squatina*, similar modifications have occurred; but the axial cartilage remains large, and the large præaxial and postaxial cartilages are directed respectively forwards and backwards, in accordance with the form of the vastly expanded fin.

In *Raia*, yet further expansion is obtained by the separation of the axial and postaxial cartilages and the interpolation of postaxial rays between them. The proximal ends of these enter into the articulation, as the great postaxial cartilage had already done.

The interpretation of the skeleton of the pectoral fin of *Chimæra* presents some difficulties. This skeleton consists (fig. 10) of:—(1) a proximal cartilage (I), which articulates by an excavated surface with the condyle of the pectoral arch; (2) a flat, curved, elongated middle cartilage (*Mt*), which is inclined backwards; (3) a small semilunar distal cartilage (*c*), which fits onto the convex distal end of the last. At the end of the convex posterior edge of the distal cartilage is a small cartilaginous ray, consisting of a long basal and a short terminal segment. Similar rays, which gradually become longer, follow this along the free convex edge of the distal cartilage and that of the middle cartilage; but the proximal end of the latter bears a much stronger ray, with a wide base (*R*), which for the most part unites with the ventral edge of the proximal cartilage (I), but is connected with the middle cartilage (*Mt*) by its posterior produced angle.

There can, I think, be no doubt that the proximal cartilage (I) in *Chimæra* answers to the proximal cartilage in *Ceratodus*. The small proximal postaxial cartilages also exactly correspond; and the large proximal præaxial rays no less closely answer to one another. But if this be so, it follows that the whole skeleton of the fin in *Ceratodus* is represented in that of *Chimæra*. The distal cartilage (*c*) in *Chimæra* is the result of the coalescence of the bases of a certain number of the postaxial rays, as is obvious on tracing the series round.

Hence it would appear that all that can represent the series of median segments except the first is the middle cartilage (*Mt*). It further seems probable that this middle cartilage in great part, if not wholly, represents the second segment of the *Ceratodus* limb. The postaxial edges, *a b* and *b c*, correspond closely; but the edge *e f*, long in *Ceratodus*, is reduced to nothing in *Chimæra*; while the edge *c d*, occupied exclusively by the third segment in *Ceratodus*, is greatly elongated and bears all the præaxial rays in *Chimæra*.

In order to change the skeleton of the pectoral fin of *Ceratodus* into that of *Chimæra*, all that will be necessary, if this comparison is correct, is that the third and following median segments of the former shall be gradually reduced, either by abortion or coalescence with the second, more and more postaxial fin-rays becoming attached to the postaxial edge of the second segment, and more and more of the præaxial rays to its præaxial edge. At the same time the first præaxial ray, enlarging backwards and forwards, intercepts the proximal ends of two or three of the following rays, and comes into connexion with the proximal segment.

The difficulty which arises out of this apparently natural interpretation of the parts of the skeleton of the fin of *Chimæra* consists in this—that it leads to a doubt as to the true nature of the postaxial cartilage (*Mt*) in *Scyllium*, and therefore in other Plagiostomes. For this metapterygial cartilage cannot at the same time represent coalesced postaxial rays, as the analogy of *Notidanus* would suggest, and the second joint of the axial skeleton, as the analogy of *Chimæra*, on the interpretation just given, indicates. If, following the analogy of *Notidanus*, we consider *Mt* in *Chimæra* to be formed of coalesced postaxial fin-rays, then the structure will present no difficulty, but will come very near that presented by the fin of *Cestracion*. The study of the development of the parts can alone solve this problem; but I am inclined provisionally to adopt the latter hypothesis, plausible as the former seems.

Polypterus and *Polyodon* furnish the best connecting links between the Plagiostome fin and that of the other Ganoidei and the Teleostei. In *Polypterus*, the *Scyllium* type is essentially preserved. In *Polyodon* and all other Ganoids of which the fin-structure is known, the type is essentially that of the Rays, in so far as fin-rays enter into the glenoid articulation behind the proximal median segment (I). These and many other special modifications of the fish's fin have been carefully worked out by Gegenbaur*, to whose excellent descriptions I have nothing to add.

If the interpretation which I have here endeavoured to make good is correct, it is clear that, as Gegenbaur has suggested, *Ceratodus* presents us with the nearest known approximation to the fundamental form of vertebrate limb, or *archipterygium*. But the asymmetry of the skeleton of the fin of *Ceratodus*, and the differences between its distal and its proximal portions, as well as the fact that the proximal median segment has no rays, appear to indicate that the veritable *archipterygium* has undergone a certain amount of modification even in *Ceratodus*. Analogy leads to the suspicion that a still more archaic fish than *Ceratodus* would have as many pairs of rays as median pieces. In this condition the skeleton would be made up of homologous segments, which might be termed *pteromeres*, each of which would consist of a *mesomere* with a præaxial and a postaxial *paramere*. And as this is the actual state of a great portion of the skeleton of the fin in *Ceratodus*, it may perhaps be permissible to carry speculation as to the primitive condition of the vertebrate limb thus far. Dr. Günther and Professor Gegenbaur go a step further, and suggest that even this *archipterygium* may be the secondary product of the coalescence of many longitudinal cartilaginous elements, which are united by their bases, while they fray out, as it were, at regular intervals towards the distal end of the limb. In this case,

* 'Untersuchungen,' Heft ii. "Brustflosse der Fische," 1865.

Gegenbaur has most ingeniously suggested that the pectoral arch, with its limb, would correspond with a branchial arch and its rays.

It will be observed that the view of the special homologies of the elements of the skeletons of the fins of fishes which I have ventured to put forth differs, fundamentally, both from that suggested by Dr. Günther and from that advanced by Gegenbaur, either in its original form or as he has modified it subsequently to the discovery of *Ceratodus*.

The former says (*l. c.* p. 533):—"When I designated the arrangement of the parts of this pectoral skeleton unique, I did not mean to convey the idea that no homological relation could be pointed out between the parts of the pectoral skeleton of *Ceratodus* and that of other fishes. It is quite evident that we have here a further development of the simple pectoral axis of *Lepidosiren* in the direction towards the Plagiostomes. The pectoral skeleton of *Lepidosiren paradoxa* consists merely of the central series of cartilages of *Ceratodus*; there is no fin-like expansion of the skin of the pectoral limb, which is a simple tapering filament. In *Lepidosiren annectens* this pectoral filament is bordered by an expansion of the skin along its lower edge; and even minute fin-rays are imbedded in each lamina of the fold; in order to support this low, one-sided, rayed fringe, very small, single-jointed cartilages are added to the axis*. The fin is still more developed in *Ceratodus*: it has become a broad, scytheshaped paddle, dilated by a fold of the skin, with two layers of finrays surrounding it in its entire circumference; therefore supporting cartilaginous branches are added on both sides of the axis; and most of the branches are composed of several joints, in order to reach the more distant parts which require the support."

This is the exact converse of the view of the relations of *Lepidosiren* and *Ceratodus* which, in agreement with Gegenbaur, I am disposed to take. The fin of the former appears to me to be a reduced and metamorphosed state of the more primitive condition retained in *Ceratodus*.

Dr. Günther goes on to say that "the arrangement of the limb-skeleton of *Ceratodus* is foreshadowed in the pectoral fin of *Acipenser*." On the contrary, in my judgment, the pectoral fin of *Acipenser* has been derived by much modification from a *Ceratodus*-like type.

In referring to those points in which I venture to dissent from Professor Gegenbaur's interpretation, I cannot refrain from expressing my sense of the very great value of his investigations into the morphology of vertebrate limbs, and my grateful indebtedness to the rich fund of new facts and new ideas which they contain. However, I found myself unable fully to accept his theory of the fish's fin and the vertebrate limb generally, in its original form; and I expressed my hesitation and its grounds in the German version of my 'Manual of the Vertebrata'†. Gegenbaur's later view is con-

* Four or five of these ray-bearers are obliquely attached to each joint of the axis (Peters, Müller's 'Archiv,' 1845, Taf. 2. fig. 2).

† 'Handbuch der Anatomie der Wirbelthiere,' übersetzt von Dr. F. Ratzel (Breslau, 1873), pp. 34, 35.

cisely stated in his 'Grundriss der vergleichenden Anatomie,' 1874, p. 493, in the following words:—

"The very various forms of the skeleton of the free limbs are deducible from a fundamental form of which only a few instances remain, and which, as representing the first and lowest condition of the fin-skeleton, I term the *archipterygium*. This is represented by a jointed cartilaginous *stem*, articulated with the pectoral arch and giving attachment, on each side, to a series of likewise jointed pieces, the *radii*. The whole structure, resembling a pinnate leaf, is singularly like the supporting apparatus of many Selachian gills, and thus throws a gleam of light upon the phylogeny of the limbs.

"*Ceratodus* presents this form of fin-skeleton, which was perhaps usual among the *Crossopterygidæ*, at present represented only by *Polypterus*. The biserial rays of the fin undergo different modifications. Among the Dipnoi the medial [postaxial] rays are retained in the form of thin rods of cartilage; while in the Selachians the lateral [præaxial] rays attain a considerable development and constitute the greater part of the massive fin-skeleton. Of the medial [postaxial] rays but few remain, though they are sufficiently distinct to sanction the assumption of a former more extensive biserial arrangement of rays on the stem of the fin."

The *metapterygium* Gegenbaur considers to answer to the axial skeleton of the *archipterygium*. The *propterygium* is formed by the union of the proximal præaxial fin-rays. The *mesopterygium* is formed by a certain number of the succeeding præaxial fin-rays.

The only part of this interpretation with which I can agree is the determination of what Gegenbaur names the propterygium as the representative of the proximal præaxial fin-ray or rays in most cases, but not in *Chimæra*, and probably not in *Notidanus*.

In my judgment, the mesopterygium of Gegenbaur is the proximal piece of the axial skeleton, which constantly retains its primary articulation with the pectoral arch. His propterygium represents the proximal præaxial fin-ray, and his metapterygium the proximal postaxial fin-ray in almost all cases; and the *ichthyopterygium*, as the typical fish-fin may be termed, differs from the archipterygium not by the more or less complete suppression of the postaxial rays, but by the general abbreviation of the whole skeleton and the gradual connexion of more or fewer fin-rays (*parameres*) with the pectoral arch.

In the effectual discharge of the function of the fish's fin, increase of breadth is needed; and this increase of surface is obtained by the gradual approximation of more and more lateral elements of the archipterygium to the shoulder-girdle.

Professor Gegenbaur has extended his theory of the limbs to the higher Vertebrata. He conceives that the axis of the archipterygium (which he considers to be the homologue of the metapterygium of the Selachian) is represented by the series of bones which is formed by the humerus, the radius, the radial segments of the carpus, and the radial digit or pollex; while the ulna, the radial segments of the carpus and the ulnar digit, the other carpal bones, and the fourth, third, and second digits represent so many præaxial rays. The very serious objection that this hypothesis makes the radius and the radial digit postaxial, while, as a matter of fact, in every vertebrate animal it is præaxial, is met by the assumption of a torsion of the humerus. But I must confess that I am wholly unable to satisfy myself of the existence of any torsion of the humerus capable of bringing about the effect attributed to it in any vertebrated animal; and, moreover, if such torsion has brought about the observed position of the manus and pes in the higher Vertebrata, any reversal of that torsion would destroy the homology of the pollex and the hallux—which is surely out of reach of doubt.

I am disposed to think, though I am far from imagining that the hypothesis can at present be demonstrated, that the higher vertebrate limb has arisen from the archipterygium in another and simpler method.

According to Gegenbaur's view, the higher vertebrate limb is the result of further progress, in the same direction, of the metamorphosis which has given rise to the ichthyopterygium. But this appears to me to be highly improbable. The ichthyopterygium is specialized *pari passu* with the other peculiarities of piscine structure, and is not developed in the Dipnoi, which are the nearest allies of the Amphibia. Moreover the higher vertebrate limb, which may be termed the *chiropterygium*, as an organ of support and prehension, requires length, strength, and mobility of its segments—conditions exactly the opposite of those which give the ichthyopterygium its special utility.

Hence, as the most highly specialized forms of ichthyopterygium result from the shortening of the skeleton of the fin, the approximation of its distal elements to the shoulder-girdle, and the multiplition of its rays, we might expect that the chiropterygium would take its origin by the lengthening of the axial skeleton, accompanied by a removal of its distal elements further away from the shoulder-girdle, and by a diminution in the number of the rays.

The parts which are traversed by a line drawn through the humerus, the intermedium, the centrale, the third distal carpal, and the third digit in the cheiropterygium may be regarded as so many mesomeres, representing the axis of the archipterygium. Two pairs of parameres are retained on each side. The præaxial are :—(1) the radius, the radiale, the first distal carpal, and the pollex; (2) the second distal carpal and the index. The postaxial parameres are :—(1) the ulna, the ulnare, the fifth distal carpal, and the digitus minimus; (2) the fourth carpal and the annularis.

In fig. 11 the skeleton of the pectoral fin of *Cestracion* is represented side by side with the skeleton of the fore limbs of *Menobranchus*, *Ichthyosaurus*, *Plesiosaurus*, and *Gecko*; and the shading of the different parts of the ichthyopterygium is repeated in what I suppose to be the homologous elements of the chiropterygium. In the case of *Menobranchus*, however, it is possible that the true pollex is suppressed, and that the actual radial digit represents the second of the pentadactyle limb, and therefore should have been left unshaded.

In accordance with the view thus suggested, the humerus in the chiropterygium is the homologue of the proximal mesomere or joint of the axis of the archipterygium, while the radius and the ulna are the homologues of the proximal ends of præaxial and postaxial parameres of the archipterygium.

The confirmation or refutation of this hypothesis is to be sought in development, and in the condition of the limbs in those Palæozoic Amphibia which may have more nearly approximated to Dipnoi than any existing or extinct forms at present known. I suggest it mainly in the hope of stimulating investigation in both these directions.

IV. *Taxonomy of* Ceratodus, *and Remarks on the Classification of Fishes.*

The indications afforded by the brain, the skull, and the limbs of *Ceratodus* are sufficient to show that it occupies a curiously central position among the Ichthyopsida, being allied on one side to the Amphibia, on another to the Chimæroidei and Plagiostomi, and on yet another to the Ganoidei—especially to that group of the Ganoids which I have termed *Crossopterygidæ*, and to the affinities of which with *Lepidosiren* I called attention in 1861.

But even *Dipterus,* which approaches *Ceratodus* and *Lepidosiren* so closely in its dentition and in the form of its fins, is far more similar to *Polypterus* and *Amia* in other respects; and there is, at present, no reason to believe that any of the Crossopterygian Ganoids possessed other than a hyostylic skull, or differed from *Polypterus* in those respects in which *Polypterus* differs from the existing Dipnoi. All known Crossopterygians have jugular plates, of which there is no trace in the Dipnoi. And as to the position of the anterior nares, which appear to have been situated on the under face of the broad snout, not only in *Dipterus,* but in *Osteolepis* and *Diplopterus,* I have shown above that, so far from being a diagnostic character of the Dipnoi, it is simply an embryonic feature retained in them, the Selachians, and very probably in many of the early Ganoidei. On the other hand, in *Amia,* there is an even closer approximation between the Ganoids and the Teleosteans than can at present be shown to exist between any Ganoids and the Dipnoi; while the differences between the Dipnoi and the Chimæroidei, and between the Chimæroidei and the Plagiostomi respectively, are not less than those between the Ganoids and the Dipnoi.

It seems to me, therefore, that by forming the Dipnoi, Ganoidei, Chimæroidei, and Plagiostomi into a group of "Palæichthyes," from which the Teleostei are excluded, as Dr. Günther proposes to do, the differences between the Teleostei and the other hyostylic fishes are brought into undue prominence, and that it is better to retain the Müllerian groups of Dipnoi (*Sirenoidei,* Müller), Ganoidei, Teleostei, Plagiostomi, and Chimæroidei (*Holocephali,* Müller) as equivalent and distinct natural assemblages.

In discussing any system of classification, however, it must be recollected that known forms certainly represent but a portion, and probably a small portion, of those which have existed, and that the most natural groups are therefore, to a great extent, the result of the influence of extraneous, and what may be properly termed accidental, conditions.

It has occurred to me that, in the present state of science, it is very desirable to have some mode of stating the facts of morphology in a condensed and comprehensible form, which shall be purely objective and free from speculation; and I now proceed to illustrate my meaning by drawing up a scheme of the morphology of the Ichthyopsida.

Looking at the animals included under this head as a whole, or at the development of any of the higher members of the group, it is observable that they present a certain series of stages of differentiation marked by the broad characters of the skull, the nature of the olfactory and respiratory organs, and the development or non-development of an opercular fold of the integument.

Thus the skull either retains its primitive segmentation (*Entomocrania*), or the primitive segmentation is lost, and a chondrocranium is developed (*Holocrania*). There are two external nostrils (*Amphirhina*) or only one (*Monorhina*).

A *pneumatocœle*, or air sac, which may become either an air-bladder or a lung, is developed (*Pneumatocœla*), or not (*Apneumatocœla*); and a fold of the integument may cover the branchial apertures (*Operculata*), or not (*Inoperculata*).

The Ichthyopsida also exhibit a series of stages of differentiation of the limbs, being either apodal or pedate; and, when pedate, having the limb-skeleton constructed upon the type of the archipterygium, or on that of the icthyopterygium, or on that of the chiropterygium.

Moreover, when the limb is an ichthyopterygium, it may possess one, or at most two basal elements, which articulate with the pectoral arch (unibasal), or there may be three (tribasal), or there may be many (multibasal), in accordance with the greater and greater divergence of the fin from the archipterygial type.

The chondrocranium may be constructed upon either the amphistylic, the hyostylic, or the autostylic plan.

Now, if the stages of general differentiation be indicated by points on a vertical line from which horizontal lines are drawn, and the stages of subordinate differentiation of the skull and limbs be indicated by points on a horizontal line from which vertical lines are drawn, we shall have vertical series of intersections indicating general differentiation, and horizontal series of intersections indicating special differentiation. Every known form will occupy some given intersections, and the unoccupied intersections will indicate unfulfilled, or unknown, possibilities of organization.

The following Table exhibits the groups of the Ichthyopsida arranged according to this scheme.

			Autostylica.			Amphistylica.	Hyostylica.		
I. HOLOCRANIA.									
A. Amphirhina.									
a. Pneumatocœla.									
1. operculata.			Amphibia (caducibranchiate).	Dipnoi.			*Polypterus.*	Most Ganoidei.	Teleostei.
2. inoperculata.			Amphibia (perennibranchiate).						
b. Apneumatocœla.									
1. operculata.					Chimæroidei.				
2. inoperculata.						*Cestracion.* *Notidanus.*	Most *Selachii.*	*Raii.*	
						Palæichthyes (Günther).			
B. Monorhina.									
1. operculata.									
2. inoperculata.		Marsipobranchii.							
II. ENTOMOCRANIA.									
1. operculata.	Pharyngobranchii.								
2. inoperculata.									
						Unibasal.	Tribasal.		Multibasal.
			Chiropterygium.	Archipterygium.		Icthyopterygium.			
	Apoda.		Pedata.						